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## Research article

### Sea crossings of migratory pink-footed geese: seasonal effects of winds on flying and stopping behaviour

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Migratory birds may need to cross barriers such as seas, without opportunities to rest or refuel. Waterbirds, unlike land birds, can stop at sea to rest or wait for better winds and thus may be less selective for supportive winds at departure and tolerate larger drift. However, pay-offs of waiting are likely to depend on circumstances (e.g. pressure for well-timed arrival, wind availability and travelling with/without juvenile brood), thus migratory behaviour during barrier crossings is expected to differ between seasons. We studied pink-footed geese *Anser brachyrhynchus* crossing the Barents Sea (ca 650 km), in spring and autumn during 2018–2020, using 94 GPS-tracks of 38 individuals, with annotated ERA5 weather data. We found that 1) especially in autumn, geese selected supportive winds for departure; 2) in spring, geese experienced lower wind support and more crosswinds than in autumn, leading to 23% longer routes, 60% longer durations, 93% longer air distances and 45% higher ratios of air-to-ground distances; 3) in both seasons, geese had more tailwinds in the first part of crossings, and in spring when deviating more from the shortest route; 4) geese stopped at sea more often in spring (mean 11×) than autumn (3×), in spring during earlier stages of crossings, but in both seasons, spent half of the crossing time at sea, during which they still continued to approach their destination slowly; 5) stops at sea happened mostly in adverse winds, warmer air, higher air humidity and on calmer water and, in autumn, took longer without juvenile brood. We conclude that for migrating pink-footed geese, Arctic capital breeders, the importance of time and energy can shift en route and that seasonal differences in wind support, flying and stopping behaviour and the pressure for a well-timed arrival cause the Barents Sea to be a larger barrier in spring than in autumn.

Keywords: breeding, ecological barrier, optimization, strategy, Svalbard, transoceanic flight



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## Introduction

Migration enables birds to exploit seasonally abundant food sources in different areas, often far apart (Alerstam et al. 2003, Newton 2008). To reach those areas, birds may need to cross ecological barriers such as oceans, deserts or mountain ridges. Barriers are characterised by the absence of opportunities to rest or replenish energy reserves by feeding (Deppe et al. 2015, Adamik et al. 2016, La Sorte and Fink 2017). Crossing a barrier therefore requires birds to sustain prolonged flights, which require additional energy reserves (Gill et al. 2009, Klaassen et al. 2011). In turn, carrying these additional fuel loads further increases the flight costs for a barrier crossing (Alerstam 2001). Thus, if birds depart in a poor body condition or if weather conditions en route turn adverse, these high energetic and physical demands during a crossing might cause mortality (Sillet and Holmes 2002, Klaassen et al. 2014, Lok et al. 2015, Loonstra et al. 2019). Also, if birds survive a crossing, they may still experience negative effects of the bad conditions during the crossing, as their arrival date may have been delayed and their body condition worsened, ultimately reducing reproductive success (Lack 1968, Drent et al. 2006, Newton 2008, Ma et al. 2011). Therefore, migratory birds that maximize the chance of successfully crossing a barrier, and have a good body condition, are expected to have higher fitness.

In line with this, many birds depart and migrate under favourable atmospheric conditions, in particular supportive tailwinds (Kerlinger and Moore 1989, Åkesson and Hedenström 2000, Dierschke and Delingat 2001, Morganti et al. 2011, Schmaljohann and Naef-Daenzer 2011, Plonczkier and Simms 2012, Åkesson et al. 2016). Birds can further adjust their migratory behaviour, specifically flight speed and compensation for winds, to handle suboptimal wind directions or changing wind conditions en route (Thorup et al. 2003, Vansteelant et al. 2017). In doing so, birds minimize the overall energy expenditure and travel time (Ahola et al. 2004, Both et al. 2005, Jonzén et al. 2006, Balbontin et al. 2009, La Sorte and Fink 2017) and maximize flight ranges and body condition upon arrival (Weber et al. 1998, Pendlebury et al. 2004, McKinney and McWilliams 2005, Ma et al. 2011).

The penalty for not sustaining flight during a sea crossing is generally fatal for land birds (Yamaguchi et al. 2012, Oppel et al. 2015), although they can incidentally rest on manmade structures such as platforms or boats (reviewed by Ronconi et al. 2015). However, waterbirds can stop at sea regularly, enabling them to rest and potentially wait for better weather conditions (Butler et al. 1998, Pennycuik et al. 1999, Griffin 2008, Hübner et al. 2010, Vissing et al. 2020). Thus, whereas land birds need to cross seas at once and are highly selective for favourable wind and weather at departure (Dierschke and Delingat 2001, Schmaljohann and Naef-Daenzer 2011, Brust et al. 2019, Bradarić et al. 2020, Manola et al. 2020), it is expected that waterbirds can afford lower selectivity at departure, and initiate stops at sea when conditions worsen for flight or orientation, or when birds get exhausted from flight.

However, for geese and swans, the decision of stopping en route at sea is expected to depend on the circumstances and therefore to differ between the migration seasons. In spring, an early arrival enables birds to start a nest that hatches at a time of high food quality (van der Graaf et al. 2006), and a good body condition upon arrival enables a high reproductive investment, especially in capital breeders (Madsen et al. 2002, Si et al. 2015, Klaassen et al. 2017). In spring, this may cause a trade-off between an early arrival and a good body condition, if reserves are limited. In autumn, such time-pressure for an early arrival is (likely) to be absent, giving geese more time to wait for supportive winds (Kölzsch et al. 2016). In addition, in autumn geese fly together with their juvenile brood (Gupte et al. 2019), which may require them to select supportive winds and stop more often. Interestingly, while Greater and Eastern greater white-fronted geese *Anser albifrons* and Bewick's swans *Cygnus columbianus bewickii* migrate faster over land in autumn than in spring due to longer stopovers (Nuijten et al. 2014, Kölzsch et al. 2016, Deng et al. 2019), there was no seasonal difference in migration duration in light-bellied brent geese *Branta bernicla brota* migrating almost non-stop over sea (Vissing et al. 2020). Furthermore, the availability of favourable winds may differ between seasons (Kislov and Matveeva 2020), as migration occurs in opposite directions. Adverse winds can increase the size of a barrier because a bird spends more energy, as it needs to fly a longer distance through the air (i.e. longer air distance) to cover a certain distance on the ground (i.e. ground distance); a longer air distance translates to higher energy expenditure. Seasonal differences in wind conditions, together with seasonal differences in time-pressure and family status, are therefore expected to shape seasonal variation in migratory behaviour during barrier crossings.

We studied the Svalbard breeding population of pink-footed geese *Anser brachyrhynchus*, which crosses more than 650 km over the open Barents Sea in spring and autumn (Glahder et al. 2006). Using 94 GPS-tracks data of 38 geese during 2018–2020, we evaluated for spring and autumn separately: 1) their selectivity for high wind support during the initiation of a crossing; 2) the distance, time and energy (measured as flight effort) required for a crossing as products of wind conditions en route; 3) how the experienced wind support en route changed with different distances and directions to crossing destinations; and 4) how often and how long geese stopped temporarily on the water, and how the timing of these stops was explained by wind, weather and water conditions, previous distances flown and travelling with a juvenile brood.

## Material and methods

### Catching, tracking and observing geese

In total, 56 pink-footed geese (5 males and 51 females) were equipped with solar-powered GPS-GSM transmitter neckbands, type OrniTrack-N38 (Ornitela UAB, Lithuania) with

a weight of 38 g (ca 1.5% of body mass) and an inner diameter of 38 mm. On a spring staging site in Tyrnävä, Oulu, Finland (64°49'40" N, 25°33'52" E), geese were caught by cannon-nets on 28 April 2018 (numbers equipped with transmitters  $n=10$ ), on 27 April 2019 ( $n=8$ ) and on 1 May 2019 ( $n=3$ ). In the Svalbard breeding areas, geese were caught in moulting family groups in a corral at Isdammen (78°12'12" N, 15°48'10" E) on 30 July 2018 ( $n=16$ ) and at Daudmannsøyra (78°13'16" N, 13°04'10" E) on 1 August 2018 ( $n=19$ ). After capture and tagging on Svalbard, geese spent more time preening than untagged geese, but this effect disappeared within approximately one week (Clausen et al. 2020). We sexed geese in the field by cloacal examination and validated this molecularly following Fridolfsson and Ellegren (1999), using blood taken from a medial metatarsal vein, primer pair 2550F/2718R and the PCR-program of Griffiths et al. (1998) and running results on a 2% agarose gel.

Transmitters recorded GPS-positions (latitude and longitude) along with, among others, the altitude (m above mean sea level, m a.s.l., ) and instantaneous speed ( $\text{m s}^{-1}$ ). Time intervals between GPS-positions varied with the battery charge of the transmitters and ranged from 10 min ( $> 75\%$  battery charge) to 1 h ( $< 25\%$ ). At high battery charge ( $> 85\%$ ), a GPS-burst of 10 GPS-positions at 1 Hz was taken to increase accuracies of altitude and speed measurements. For further analysis, we kept the single GPS-positions and the last position of each GPS-burst. Time intervals of all individuals mostly ranged between 10 and 30 min (for GPS-positions with time intervals  $< 65$  min (99% of all GPS-positions): median = 10.3 min, mean =  $12.3 \pm 6.8$  SD, range = 1–61.5; Supporting information).

A track was defined as a crossing of the Barents Sea, starting at the first and ending at the last GPS-positions above sea. GPS-positions above sea were defined as not falling within convex hulls of the coastlines of Scandinavia and Svalbard (and the islands of Bjørnøya, Hopen and Svenskøya). Tracks during both seasons had similar coverages, as the (sum of) distances per track from the convex hull at departure to the first GPS-position and from the last GPS-position to the convex hull at destination did not differ significantly between spring (median = 31 km, mean =  $40 \pm 35$  SD) and autumn (median = 54 km, mean =  $72 \pm 58$  SD; Wilcoxon rank sum test:  $W=573$ ,  $p=0.082$ ). Additionally, we used those convex hulls to exclude GPS-positions of geese during migration above water that followed the coastlines of Norway and Svalbard before starting an actual crossing, which were not considered as part of a track. Based on this, we calculated the distance (km) and duration (h) of each track in QGIS (ver. 3.4.5). For each track, the departure location was defined as the location on land, closest to the first GPS-position above sea. For each GPS-position, the destination was defined as the nearest point on the convex hull of the coastlines on the opposite side of a crossing; that is, the shortest route possible.

We excluded incomplete tracks ( $n=24$ ) and 2 out of 3 non-independent tracks (a pair with a young migrating together of which only the mother was included). Furthermore, tracks with large time gaps ( $> 3$  GPS-positions with time intervals

$> 60$  min and a total gap of  $> 10$  h;  $n=6$ ) and tracks that did not belong to the Svalbard breeding population ( $n=47$ ) were excluded. Overall, this resulted in 14633 GPS-positions of 94 tracks from 38 geese which migrated to Svalbard in spring (pre-breeding;  $n=45$ ) and to Norway in autumn (post-breeding;  $n=49$ ) in 2018 (spring:  $n=5$ ; autumn:  $n=31$ ), 2019 (spring:  $n=24$ ; autumn:  $n=8$ ) and 2020 (spring:  $n=16$ ; autumn:  $n=10$ ).

All geese were observed at least once during autumn migration in Norway, Sweden, Denmark, Netherlands and/or Belgium, to see if they were accompanied by a juvenile brood, which travel with their parents up to early spring in geese (Gupte et al. 2018). Professional and amateur bird watchers entered these sightings into the citizen science platform www.geese.org (Ebbinge et al. 2020). In 2018, 13 out of 36 geese of which the crossing was tracked were seen with juvenile brood in autumn. In 2019, this was 0 out of 32, and for 2020 this was 3 out of 26. The rest were seen without juvenile brood.

## Flight classification and behaviour

To distinguish flight from non-flight, we used the instantaneous ground speed measurements of the transmitters. We regarded the instantaneous ground speed  $V_i$  more reliable to indicate flight than the calculated ground speed  $V_{nl}$  (towards the subsequent GPS-position), because  $V_{nl}$  was sometimes inaccurate due to landings and take-offs between GPS-positions. Still,  $V_i$  and  $V_{nl}$  were significantly correlated (Pearson correlation coefficients:  $r=0.78$ ,  $t=91.838$ ,  $df=5269$ ,  $p < 0.01$  for  $V_i$  and  $V_{nl} > 5.6 \text{ m s}^{-1}$ ).  $V_i$  was bimodally distributed, with a low at  $4.2 \text{ m s}^{-1}$  ( $= 15 \text{ km h}^{-1}$ ; Supporting information), which was taken as cutoff for non-flight ( $< 4.2 \text{ m s}^{-1}$ ) and flight behaviour ( $\geq 4.2 \text{ m s}^{-1}$ ). This resulted in 5631 GPS-positions during flights (mean  $V_i = 15.6 \text{ m s}^{-1} \pm 5.0$  SD) and 9002 during non-flights.

To describe stops at sea in detail based on accurate and unbiased duration calculations, only tracks with time intervals between GPS-positions  $< 3$  h were included ( $n=50$ , time intervals: median = 10.4 min, mean = 11.9). The durations of stops were taken as the time difference between the first and last GPS-position, plus half the intervals before the first and after the last. Distances moved during stops at sea were then calculated from extrapolation of speeds; because of the low speeds on water, with little variation (thus low resolution), we took  $V_i$  only when a stop contained 1 or 2 GPS-positions, and  $V_{nl}$  when a stop contained at least 3 GPS-positions, as this measure is expected to have better resolution in this case.

## Environmental data and flight altitude

To obtain environmental data for the GPS-positions of geese, we used the Env-DATA Track Annotation Service as described by Dodge et al. (2013) using data of the European Centre for Midrange Weather Forecast (ECMWF) based on the ERA5 reanalysis. The temporal resolution was  $\text{h}^{-1}$ , spatial resolution

of all data was  $0.25^\circ$  except for data regarding waves with a spatial resolution of  $0.5^\circ$  (for a description of each parameter see Supporting information). We used a bilinear interpolation method.

To link GPS-positions to environmental data, flight altitudes need to be known. However, above sea, the altitude measurements by the transmitters showed large outliers, including negative values, presumably due to reflections of the water surface. We therefore determined the most probable flight altitude above sea assuming similar flight altitudes as above land. For large birds like pink-footed geese, climbing to high altitudes is more costly in terms of energy expenditure and thus less likely than for smaller birds (Klaassen et al. 2004). Similar species, like brent geese *Branta bernicla*, are known to usually fly at low altitudes  $< 100$  m a.s.l. (Alerstam et al. 1990) and Bewick's swans were found to fly lower above sea than above land (Klaassen et al. 2004). Furthermore, frequent stops at sea suggest that pink-footed geese do not fly at high altitudes at all. To confirm this, we assessed the undistorted altitude measurements of GPS-bursts of flying geese above land. Within each GPS-burst, altitude measurements varied, but stabilized towards the end. Altitude measurements of the last 4 GPS-positions within GPS-bursts indicated flight altitudes of pink-footed geese between 1 and 2281 m a.s.l. (mean = 225, median = 127; excluding negative values) with most (= 87%)  $< 500$  m a.s.l. (Supporting information).

First, wind data (U- and V-component given the E-W and S-N winds;  $m\ s^{-1}$ ) were obtained for six altitudes: 10, 111 (= 1000 mbar), 323 (= 975 mbar), 540 (= 950 mbar), 762 (= 925 mbar) and 1457 m a.s.l. (= 850 mbar). To test whether wind conditions differed between altitudes, Pearson correlation coefficients were calculated between altitudes of the respective wind component (U- and V-). Wind conditions of all altitudes were significantly correlated, for both the U- (Pearson correlation coefficients: all pairwise correlations:  $r > 0.87$ ,  $n = 16815$ , all  $p < 0.001$ ) and V-component (Pearson correlation coefficients: all pairwise correlations:  $r > 0.79$ ,  $n = 16815$ , all  $p < 0.001$ ). Winds between 10 and 540 m a.s.l., in particular, did not differ (U-component: all  $r > 0.95$ , all  $p < 0.001$ ; V-component: all  $r > 0.94$ , all  $p < 0.01$ ). In this study we used wind conditions at an altitude of 111 m a.s.l. as this probably matches flight altitudes of geese above sea best.

To test how other environmental data determine the location and timing of stops at sea, we additionally obtained the mean wave direction ( $^\circ$ ), mean wave period (s), wave height (m; all at surface level), relative air vorticity ( $s^{-1}$ ), relative air humidity (%) and air temperature ( $^\circ C$ ; for 111 m a.s.l., Supporting information).

### Calculation of wind components

To describe how the wind was blowing in relation to the displacement direction of a goose, we used the obtained U- and V-components of winds to calculate the wind speed  $V_w$ , wind support  $W_s$ , crosswinds  $W_c$  and airspeed  $V_a$  following the approach of Safi et al. (2013). The displacement direction was defined as the calculated direction  $D_{ni}$  between

subsequent GPS-positions ( $0^\circ$  as north). Crosswinds  $W_c$  were calculated as the wind speed  $V_w$  decomposed perpendicular to the ground speed  $V_i$ . The airspeed  $V_a$  defined actual flights ( $m\ s^{-1}$ ) of geese, thus irrespective of the wind speed  $V_w$ . The wind support  $W_s$  ( $m\ s^{-1}$ ) was given as the wind speed  $V_w$  decomposed in the direction of the ground speed  $V_i$  (transformed to  $m\ s^{-1}$ ); geese experienced tailwinds when  $W_s > 0$  and headwinds when  $W_s < 0$ .

For each GPS-position and departure location, we also calculated the available wind supports  $W_{smd}$  and crosswinds  $W_{cmd}$  in relation to the shortest route to the migration destination possible. To assess whether available wind conditions differed between days, we additionally obtained wind parameters and calculated  $W_{smd}$  and  $W_{cmd}$  for the daytime of the actual initiation of the crossing for each of the 5 days before the actual initiation and for each of the 5 days after.

For each track (t), we calculated the average wind support  $W_s$  during flights (Eq. 1) and the average crosswinds  $W_c$  during flights (Eq. 2;  $m\ s^{-1}$ ) over all GPS-positions (i), from the first to the second-last one ( $n - 1$ ):

$$\text{Average wind support}_t = \frac{\left(\sum_{i=1}^{n-1} (\text{wind support}_i \times \text{time}_{i+1})\right)}{\text{Flight duration}_t} \quad (1)$$

$$\text{Average crosswinds}_t = \frac{\left(\sum_{i=1}^{n-1} (\text{crosswind}_i \times \text{time}_{i+1})\right)}{\text{Flight duration}_t} \quad (2)$$

We used the airspeed  $V_a$  as a measure for the flight effort, i.e. the energy expenditure during flights (Pennycuik 1978). The total air distance (Eq. 3; km) per track was calculated as an absolute measure:

$$\text{Total air distance}_t = \left(\sum_{i=1}^{n-1} (\text{airspeed}_i \times \text{time}_{i+1})\right) \quad (3)$$

To calculate a measure for the relative energetic costs, we related the total air distance to the ground distance of tracks, which can be seen as the proportion of the route flown by own power (Eq. 4; %):

Ratio air distance to ground distance<sub>t</sub> =

$$\frac{\text{Total air distance}_t}{\text{Ground distance}_t} \times 100\% \quad (4)$$

Furthermore, the decision of a goose to fly or to stop may depend not only on the current but also on the previously experienced wind conditions during flights which can lead to exhaustion. We calculated the air distance between two stops on sea (Eq. 5) based on all GPS-positions during flights (j) between the stops (where  $j = 0$  denotes the last GPS-position of the last stop) as:



$$\text{Air distance since last stop}_j = \left( \sum_{j=1}^n (\text{airspeed}_j \times \text{time}_{j-1}) \right) \quad (5)$$

Lastly, we calculated the extent of detour (Eq. 6; %) for each track as the deviation of the actual route from the shortest route possible at departure, as:

$$\text{Detour}_t = \frac{\text{Ground distance}_t}{\text{Distance of shortest route at departure}_t} \times 100\% \quad (6)$$

To test for differences in the wind support  $W_s$  per GPS-position in relation to deviations and the track's progress, we calculated the deviation  $\Delta D$  ( $0$ – $180^\circ$ ) of the actual displacement direction  $D_{nl}$  from the calculated direction of the shortest route possible ( $0^\circ$  as north). Additionally, we calculated the deviation of the wave direction from  $D_{md}$ . Further, we defined the track's progress as the percentage of covered ground distance along a track until each GPS-position.

### Statistical analysis

To compare available wind conditions between the 5 days before actual initiations of crossings, the days of the initiations and the 5 days after that, we fitted linear mixed models (LMMs) using the lmer-function of the 'lmerTest' package (Kuznetsova et al. 2017); all analyses were conducted in R (<[www.r-project.org](http://www.r-project.org)>) using the RStudio interface (ver. 1.2.5033). For spring and autumn separately, we modelled the available wind support  $W_{smd}$  – (LMM1 for autumn; LMM2 for spring) and the crosswinds  $W_{cmd}$  in relation to the shortest route to destination possible (LMM3 for spring; LMM4 for autumn) as a function of the days to departure (fixed effect), track ID and year (random effects). To test for overall effects of days to departure, we used analysis of variance (ANOVA); if overall effects were significant ( $p < 0.05$ ), we applied post-hoc tests (Sidak).

To assess seasonal differences on track level, we modelled the average wind support  $W_s$  during flights (LMM5), average crosswinds  $W_c$  during flights (log-transformed; LMM6), detour (log-transformed; LMM7), ground distance (log-transformed; LMM8), air distance (log-transformed; LMM9), ratio air distance to ground distance (LMM10) and duration (log-transformed; LMM12) as a function of migration period (fixed effect) and individual goose (random effect) using the glmmTMB-function of the 'glmmTMB' package (Brooks et al. 2017). We also tested for the effect of flying with juvenile brood (fixed effect) on the ratio of air distance to ground distance in autumn (LMM11) with individual goose (random effect). For models including air distance (LMM9, 10 and 11), we only used tracks with time gaps of < 3 h.

Furthermore, we modelled the wind support  $W_s$  during flights per GPS-position as a function of the deviations  $\Delta D$  and the track's progress (fixed effects), both interacting with migration period (LMM13). Here, random effects were track ID nested in individual goose and crossed over year. All

variables including directions or angles were transformed into circular variables and correlations were assessed following the approach of Mardia and Jupp (2000) using the 'Directional' package (Tsagris et al. 2021). We fitted two models with the same random effect structure as for LMM13 to test whether flight distances between stops at sea (log-transformed) differed between migration periods (fixed effect; LMM14) and between geese flying with or without juvenile brood (fixed effect; only for autumn; LMM15).

Further, we fitted two mixed effect logistic regression models (MELRs) for flight in geese (0 = non-flight; 1 = flight) as previously classified. The first model (MELR1) tested for effects of migration periods, percentages of covered ground distances until each GPS-position and the available wind support  $W_{smd}$  in relation to the shortest route (fixed effects); the random effect structure of LMM13 was implemented. The second model (MELR2) tested for effects of environmental parameters, which were standardized (z-transformed) beforehand to ensure comparable effect sizes and were the temperature, relative humidity, relative vorticity, mean wave period, wave height and the wave direction deviation. Environmental parameters were dredged (Barton 2009), constructing and comparing all possible additive models ( $n = 62$ ) including up to five variables, and the simplest model within 2  $\Delta AICc$  was selected as MELR2 (for a description of all models see Supporting information). Random effects were track ID nested in individual goose and crossed over period (i.e. spring or autumn in a given year;  $n = 6$ ).

## Results

### Wind conditions during crossing initiation

Pink-footed geese initiated crossings of the Barents Sea to Svalbard in spring between 9 and 21 May ( $n = 45$ ) and to Norway in autumn between 12 and 27 September ( $n = 49$ ; Supporting information). Initiations occurred at any time of the day, but mostly took place between 07:00 and 13:00 (local time: UTC + 2) which was non-random (Rayleigh Test of uniformity: test statistic = 0.3607,  $p < 0.001$ ). Starting times in spring (circular mean =  $11:58 \pm 5:17$  SD; Rayleigh Test of uniformity: test statistic = 0.3844,  $p = 0.001$ ) and autumn (circular mean =  $12:48 \pm 5:35$  SD; Rayleigh Test of uniformity: test statistic = 0.3430,  $p = 0.003$ ) did not differ significantly (circular ANOVA:  $F_{1,93} = 0.465$ ,  $p = 0.497$ ).

In general, the available wind support towards destinations during actual initiations of crossings was significantly higher in autumn (mean =  $5.4 \text{ m s}^{-1} \pm 3.6$  SD) than in spring (mean =  $2.7 \text{ m s}^{-1} \pm 4.4$  SD; Welch Two Sample t-test:  $df = 85.152$ ,  $t = 3.133$ ,  $p = 0.002$ , Fig. 1). However, during the five preceding and five following days, the available wind support towards destinations was significantly higher in spring (mean =  $0.8 \text{ m s}^{-1} \pm 5.1$  SD) than in autumn (mean =  $-0.2 \text{ m s}^{-1} \pm 5.4$  SD; Welch Two Sample t-test:  $df = 937.3$ ,  $t = 3.094$ ,  $p = 0.002$ ). Among the 11 days

around a goose's initiation of crossing (five preceding days, day of initiation and five following days), the available wind supports towards destination varied significantly in autumn (ANOVA LMM1:  $df=10$ ,  $F=8.766$ ,  $p < 0.001$ ), but not in spring (ANOVA LMM2:  $df=10$ ,  $F=1.713$ ,  $p=0.071$ ). In autumn, geese always initiated crossings with significantly higher available wind supports towards destinations than they would have had at the same time of the day during the five preceding (Sidak post-hoc test LMM1: all  $t < 5.838$ , all  $p < 0.001$ ) or five following days (Sidak post-hoc test LMM1: all  $t > 5.748$ , all  $p < 0.001$ ). This was in contrast to spring, where available wind supports towards destinations during actual crossing initiations were significantly higher than those of only 1 out of 10 days (Sidak post-hoc test LMM7:  $t=3.300$ ,  $p=0.04$ ), namely the day after the actual initiation, but not significantly different from the other 9 days (Fig. 1).

Crosswinds in relation to the shortest route to destination during actual initiations of crossings did not differ significantly between spring (mean =  $0.3 \text{ m s}^{-1} \pm 6.6 \text{ SD}$ ) and autumn (mean =  $2.1 \text{ m s}^{-1} \pm 6.2 \text{ SD}$ ; Wilcoxon rank sum test:  $W=903$ ,  $p=0.132$ ). However, these crosswinds differed significantly among the 11 days around initiations of crossings in spring (ANOVA LMM3:  $df=10$ ,  $F=3.339$ ,  $p < 0.001$ ), but not in autumn (ANOVA LMM4:  $df=10$ ,  $F=1.069$ ,  $p=0.385$ ), although in spring these crosswinds did not vary significantly with respect to those during actual initiations (Sidak post-hoc test LMM3:  $0.010 < \text{all } t < 1.891$ , all  $p > 0.751$ ).

In autumn, 16 crossings were initiated together with an own juvenile brood and 33 without. These crossings were initiated with slightly higher available wind supports towards the destination (mean =  $6.3 \text{ m s}^{-1} \pm 4.2 \text{ SD}$ , median = 6.7) than crossings without juvenile brood (mean =  $4.9 \text{ m s}^{-1} \pm 3.3 \text{ SD}$ , median = 5.7), but this difference was not significant (Wilcoxon rank sum test:  $W=341$ ,  $p=0.103$ ).

## Crossings in relation to wind support and crosswinds

Large seasonal differences were found in crossing characteristics and the wind support (Fig. 2). The average wind support during flights in spring (mean =  $0.2 \text{ m s}^{-1} \pm 2.3 \text{ SD}$ ) was significantly lower, by  $5.9 \text{ m s}^{-1}$ , than in autumn (mean =  $6.1 \pm 2.6 \text{ SD}$ ; LMM5:  $df=1$ ,  $z=-9.709$ ,  $p < 0.001$ ; Fig. 3). In spring, geese also experienced slightly stronger average crosswinds during flights (mean =  $7.2 \text{ m s}^{-1} \pm 3.3 \text{ SD}$ ) than in autumn (mean =  $5.8 \pm 3.4 \text{ SD}$ ), even though this difference was only near-significant (LMM6:  $df=1$ ,  $z=1.807$ ,  $p=0.071$ ).

Generally, geese crossed the Barents Sea significantly less straight, i.e. had a 18% larger detour extent from the shortest route between departure and destination, in spring (mean =  $122\% \pm 39 \text{ SD}$ , max = 313) than in autumn (mean =  $104\% \pm 20 \text{ SD}$ , max = 140; LMM7:  $df=1$ ,  $z=3.540$ ,  $p < 0.001$ ; Fig. 3). Furthermore, during spring crossings, geese covered 181 km longer ground distances (mean =  $980 \text{ km} \pm 268 \text{ SD}$ ) and 519 km longer air distances (mean =  $1116 \text{ km} \pm 495 \text{ SD}$ ) than during autumn crossings (ground distances: mean =  $799 \text{ km} \pm 151 \text{ SD}$ ; LMM8:  $df=1$ ,  $z=2.360$ ,  $p=0.018$ ; air distances: mean =  $597 \text{ km} \pm 158 \text{ SD}$ ; LMM9:  $df=1$ ,  $z=7.750$ ,  $p < 0.001$ ; Fig. 3). By this, the ratio of the air distance to ground distance differed significantly between the seasons due to wind support, when geese in spring flew 35% of the ground distance more by own power to cross the Barents Sea (mean =  $110\% \pm 24 \text{ SD}$ , range = 48–167) compared to autumn (mean =  $76\% \pm 17 \text{ SD}$ , range = 48–111, LMM10:  $df=1$ ,  $z=-1.428$ ,  $p=0.153$ ). Travelling with a juvenile brood affected this ratio near-significantly (with: mean =  $80\% \pm 16 \text{ SD}$ , without: mean =  $65 \pm 17 \text{ SD}$ ; LMM11:  $df=1$ ,  $z=1.951$ ,  $p=0.051$ ). Moreover, the duration of crossings was significantly longer in spring (mean =  $67 \text{ h} \pm 115 \text{ SD}$ , range = 16–795) than in

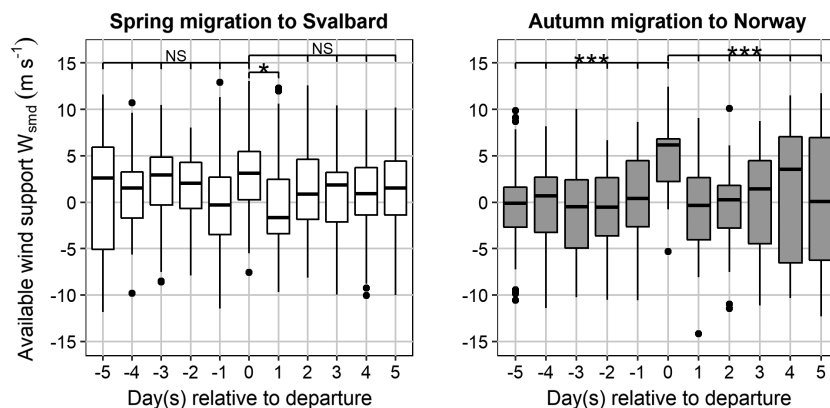


Figure 1. Wind support towards the migration destination at the time when pink-footed geese initiated their Barents Sea crossing. The available wind support  $W_{\text{smd}}$  in the direction of the migration destination, i.e. along the shortest possible route crossing the Barents Sea, was in autumn (right panel,  $n=49$ , 2018–2020) significantly higher during departures ( $t=0$ ) than at the same time during the five preceding ( $t < 0$ ) or following ( $t > 0$ ) days. In spring (left panel,  $n=45$  tracks, 2018–2020),  $W_{\text{smd}}$  at departure was only higher than that during the following day, but in general  $W_{\text{smd}}$  on non-departure days was higher in spring than autumn. NS: not significant, \*:  $p < 0.05$ , \*\*\*:  $p < 0.001$ .

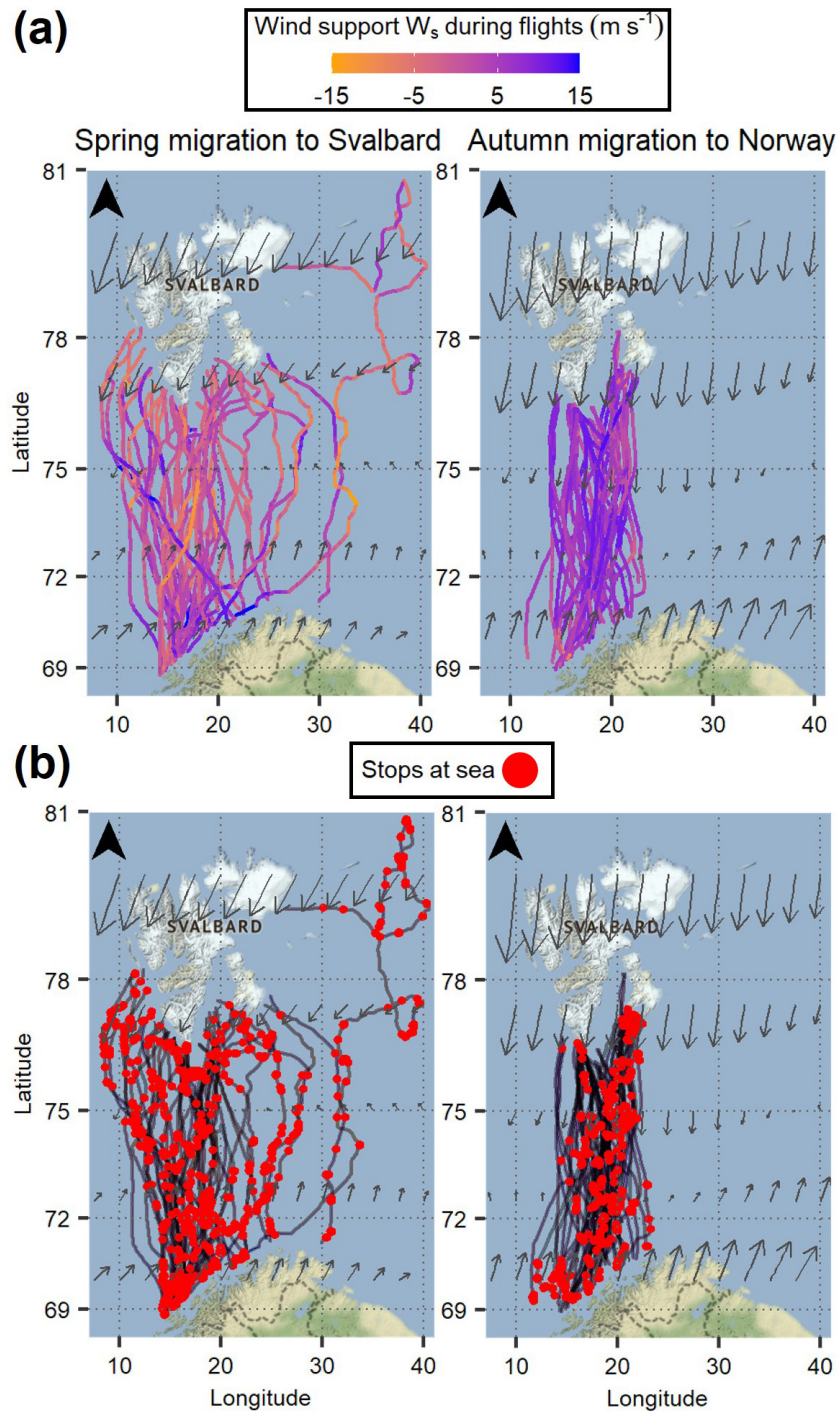


Figure 2. Tracks of pink-footed geese crossing the Barents Sea. The wind support during flights (top panels;  $\text{m s}^{-1}$ ; negative values indicating headwinds and positive values tailwinds) was lower during spring (left;  $n=45$  tracks, 2018–2020) than during autumn (right;  $n=49$ , 2018–2020). In spring, geese deviated more from the shortest route and one goose seemed disoriented, migrating far north up to the Arctic Ocean. Both in spring and autumn, geese stopped at sea (bottom panels; red dots) and the occurrence of these stops was related to wind, weather and water conditions, and family status. Arrows are only for visualization and indicate average wind regimes (average U- and V-components per month) during May (spring) and September (autumn) for the period 2018–2020 based on wind data (height = 111 m a.s.l., temporal resolution = 6 h, spatial resolution =  $2.5^\circ$ ) from the NCEP/NCAR reanalysis acquired with the ‘RNCEP’ package (Kemp et al. 2011).

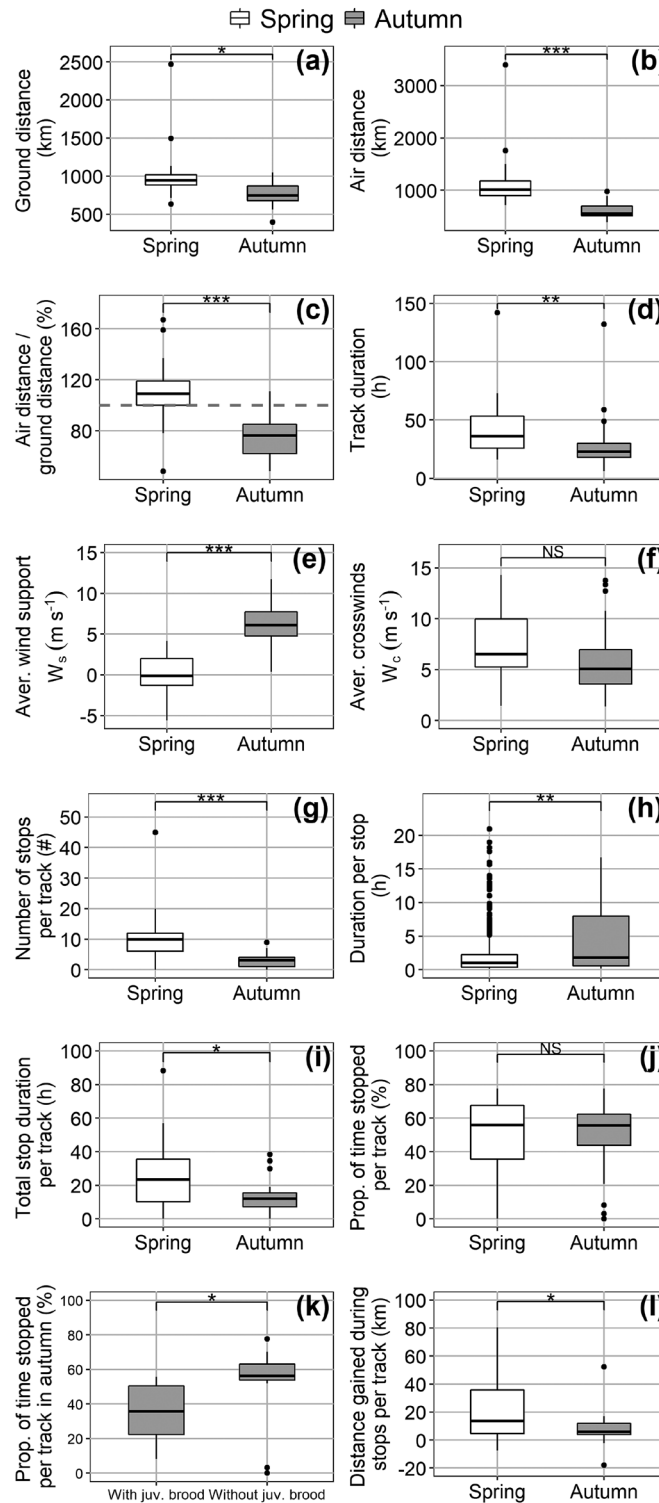


Figure 3. Features of crossings of pink-footed geese over the Barents Sea between 2018 and 2020. In spring ( $n = 45$  tracks), geese experienced less wind support (panel e) but similar crosswinds (panel f), leading to longer ground (panel a) and air distances (panel b), and a higher air distance/ground distance ratio (panel c; an indication for the proportion of a crossing flown by own power, with the red dotted line indicating 100%) than in autumn ( $n = 49$ ). Also the duration of crossings was longer in spring (panel d), partly because of a longer total stop duration in spring (panel i) as a result of more frequent (panel g) but shorter stops in spring (panel h). Although there was no difference between seasons in the proportion of the crossing duration that geese spent on the water (panel j), this did differ in autumn between geese with and without a juvenile brood flying along (panel k). During stops at sea, geese were usually displaced towards their destination in both seasons (panel l). NS: not significant, \*:  $p > 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .



autumn (mean = 42 h  $\pm$  44 SD, range = 6–244; LMM12:  $df=1$ ,  $z=3.21$ ,  $p=0.001$ ; Fig. 3).

Wind support in relation to location and heading during crossings

In autumn, the wind support was significantly lower when geese deviated more from the shortest route (LMM13: standardized  $\beta=-1.124 \pm 0.167$  SE,  $df=1$ ,  $z=-6.743$ ,  $p < 0.001$ ), but mostly still higher than the wind support in spring at similar percentage of track distance covered. In contrast, in spring geese flew with significantly higher wind supports when deviating from the shortest route (LMM13: standardized  $\beta=2.235 \pm 0.180$  SE,  $df=1$ ,  $z=12.428$ ,  $p < 0.001$ ) During spring crossings, geese deviated significantly more from the shortest route (mean = 23°  $\pm$  24 SD, median = 17) than during autumn crossings (mean = 16°  $\pm$  18 SD, median = 12; Welch Two Sample t-test:  $df=1448.2$ ,  $t=7.593$ ,  $p < 0.001$ ). Geese experienced higher wind support during earlier stages of crossings, both in spring (LMM13:  $\beta=-0.021 \pm 0.005$  SE,  $df=1$ ,  $z=-4.457$ ,  $p < 0.001$ ) and in autumn, even though this effect was significantly weaker in autumn compared to spring (LMM13:  $\beta=-0.024 \pm 0.004$  SE,  $df=1$ ,  $z=-5.932$ ,  $p < 0.001$ ). The model (LMM13) explained 51% of the variation in wind support  $W_s$  during flights.

### Circumstances during stops at sea

Both in spring and autumn, geese stopped on the water (Fig. 2). These stops were initiated at all times of the day, but with a broad peak in the (early) afternoon in both seasons (spring: circular mean = 13:15  $\pm$  6:41 SD local time: UTC + 2; Rayleigh test of uniformity: test statistic = 0.203,  $p < 0.001$ ; autumn: circular mean = 15:49  $\pm$  6:49 SD; Rayleigh test of uniformity: test statistic = 0.204,  $p=0.069$ ), so, slightly earlier in spring than autumn (circular ANOVA:  $F_{1,381}=5.799$ ,  $p=0.017$ ). In spring and autumn, geese re-initiated flights mostly in the morning until early afternoon (spring: circular mean = 11:37  $\pm$  6:41 SD; Rayleigh test of uniformity: test statistic = 0.201,  $p < 0.001$ ; autumn: circular mean = 07:06  $\pm$  6:02 SD; Rayleigh test of uniformity: test statistic = 0.287,  $p=0.005$ ), thus later in spring than in autumn (circular ANOVA,  $F_{1,381}=23.25$ ,  $p < 0.001$ ).

Geese made more stops on water during a crossing in spring (mean = 11 times  $\pm$  8.4 SD, range = 0–45) than in autumn (mean = 3 times  $\pm$  2 SD, range = 0–9; Wilcoxon rank sum test:  $W=63.5$ ,  $p < 0.001$ ; Fig. 3). However, the duration per stop was significantly shorter in spring (mean = 2.2 h per stop  $\pm$  3.4 SD, range = 0.09–21.0; autumn: mean = 4.3 h per stop  $\pm$  5.1 SD, range = 0.17–16.7; Wilcoxon rank sum test:  $W=12314$ ,  $p=0.002$ ). Still, per crossing, this amounted in a significantly longer total stop duration on water in spring (mean 24.7 h  $\pm$  20.4 SD, range = 0–88.2) than in autumn (mean 13.3 h  $\pm$  10.4 SD, range = 0–38.3; Wilcoxon rank sum test:  $W=196.5$ ,  $p=0.05$ ). Thus, in both seasons, stops at sea took on average about half of the total duration of a crossing, which did not differ between seasons (spring: mean = 49%  $\pm$  22 SD, range = 0–78; autumn: mean = 48  $\pm$

22 SD, range = 0–78; Wilcoxon rank sum test:  $W=279.5$ ,  $p=0.78$ ). During autumn crossings, geese with a juvenile brood stopped at sea for a shorter proportion of time (mean 35%  $\pm$  19, range 8–56) than geese without juvenile brood (mean 52%  $\pm$  23 SD, range 1–78, Wilcoxon rank sum test:  $W=17$ ,  $p=0.041$ ; Fig. 3). Geese with or without juvenile brood did not differ in the number of stops, duration per stop, total stop duration, speed during stops or distance covered or gained during stops (Supporting information). Geese mostly flew short distances between two stops on water (spring: mean = 100 km  $\pm$  126 SD, median = 52; autumn: mean = 111  $\pm$  115 SD, median = 62) compared to the observed maxima (spring: 4–827 km; autumn: 2–524; for a histogram see Supporting information). These air distances between stops did not differ significantly between seasons (LMM12:  $df=1$ ,  $z=-1.720$ ,  $p=0.086$ ) and between geese flying with and without juvenile brood (LMM13:  $df=1$ ,  $z=-0.094$ ,  $p=0.925$ ).

The probability for a goose to fly (and not to stop at sea) at a given GPS-location was significantly higher in spring than in autumn (MELR1:  $df=1$ ,  $z=4.705$ ,  $p < 0.001$ ; Fig. 4). In both seasons, geese had significantly higher flight probabilities when the available wind support in the direction of the shortest route was higher (MELR1:  $df=1$ ,  $z=9.252$ ,  $p < 0.001$ ). Furthermore, in spring, geese had higher flight probabilities during later stages of crossings (MELR1:  $df=1$ ,  $z=4.079$ ,  $p < 0.001$ ) but, in autumn, progress of the crossings did not affect flight probabilities (MELR1:  $df=1$ ,  $z=0.354$ ,  $p=0.723$ ; Fig. 4). The model (MELR1) predicted 65% of flight correctly and explained 20% of the variation.

When modelling flight probabilities separately as a function of other environmental conditions (model weight best model = 0.988, model weight second model = 0.008 and  $\Delta AICc=9.62$ ; Supporting information), we found that, on the one hand, geese in both seasons had significantly higher flight probabilities when mean wave periods were longer (MELR2:  $df=1$ ,  $z=3.628$ ,  $p < 0.001$ ), waves higher (MELR2:  $df=1$ ,  $z=4.020$ ,  $p < 0.001$ ) and the relative air vorticity stronger (MELR2:  $df=1$ ,  $z=5.777$ ,  $p < 0.001$ ; Fig. 4). Geese had lower flight probabilities when the relative air humidity was higher (MELR2:  $df=1$ ,  $z=-20.750$ ,  $p < 0.001$ ) and on average interrupted flights at a relative humidity of 76% in spring and autumn. In autumn, higher temperatures significantly decreased flight probabilities (MELR2:  $\beta=-1.57 \pm 0.07$  SE,  $df=1$ ,  $z=-22.760$ ,  $p < 0.001$ ) which dropped below 0.5 at  $> 4^\circ\text{C}$ . However, this effect was significantly less strong in spring (MELR2:  $\beta=0.45 \pm 0.08$  SE,  $df=1$ ,  $z=5.854$ ,  $p < 0.001$ ; Fig. 4) when flight probabilities dropped below 0.5 at a higher temperature ( $> 7^\circ\text{C}$ ). The model (MELR2) predicted 75% of flight correctly and explained 38% of the variation.

The displacement speed during stops at sea did not differ between the seasons (spring: mean = 0.6 m s<sup>-1</sup>  $\pm$  0.7 SD, range = 0–3.9; autumn: mean = 0.6  $\pm$  0.7 SD, range = 0–3.9; Wilcoxon rank sum test:  $W=9707.5$ ,  $p=0.85$ ). Per stop, geese moved for an average distance of 4.0 km in spring ( $\pm$  7.4 SD, range = 0–61.1) and 5.7 km in autumn ( $\pm$  5.7

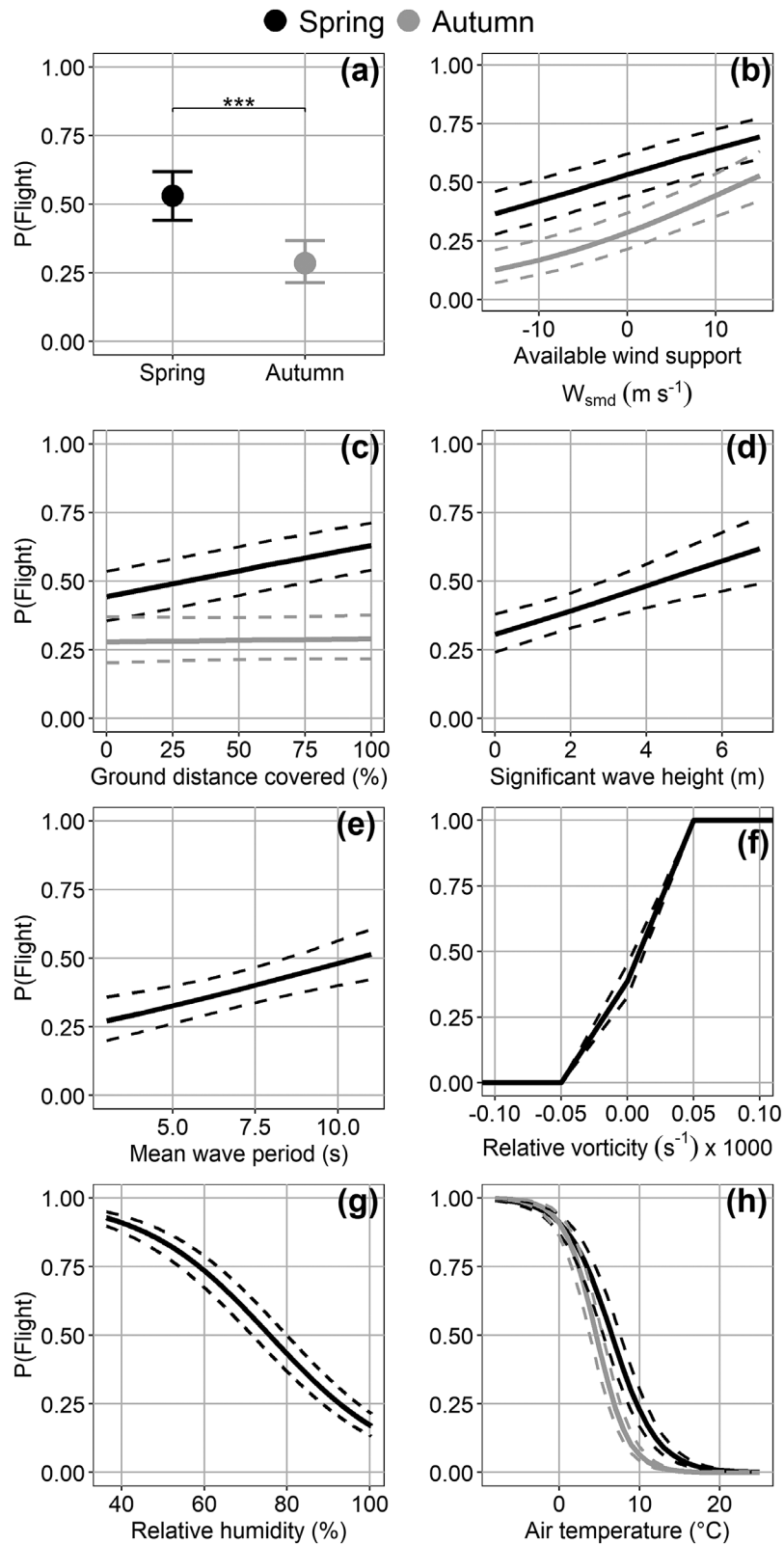


Figure 4. Circumstances explaining the probability of pink-footed geese to be in flight at a given location during a Barents Sea crossing. Flight probabilities (1 = flight, 0 = stop at sea) between 2018 and 2020, as modeled with MELR1, were higher in spring (black;  $n = 45$  tracks) than in autumn (grey;  $n = 49$ , panel a) and in both seasons increased with available wind support (panel b) and only in spring when the geese approached their destination (panel c). In a separate model, MELR2, flight probability was found to covary with the significant wave height (panel d), mean wave period (panel e), relative vorticity (panel f), relative humidity (panel g) and air temperature (panel h). Significance \*\*\*:  $p < 0.001$ .

SD, range=0–22.4; Wilcoxon rank sum test:  $W=12274$ ,  $p=0.02$ ). During a total crossing, geese covered more distance on water during spring (mean 43.9 km  $\pm$  38.7 SD, range=0–131.3) than in autumn (mean 17.3 km  $\pm$  11.9 SD, range=0–44.0 SD; Wilcoxon rank sum test:  $W=169$ ,  $p=0.01$ ). Interestingly, geese on water were often displaced in the direction of the track's destination: the average difference between the displacement direction and the direction to the track's destination was in spring  $-17.8^\circ$  ( $\pm$  74.6 SD, range= $-174.5$  to 173.4, Rayleigh test of uniformity: test statistic=0.435,  $p < 0.001$ ) and in autumn  $16.7^\circ$  ( $\pm$  65.7 SD, range= $-174.7$  to 152.5, Rayleigh test of uniformity: test statistic=0.559,  $p < 0.001$ ). However, the goose's heading did not correlate with the direction towards the destination (spring: correlation coefficient for angular variables=0.008,  $p=0.901$ ; autumn: correlation coefficient for angular variables= $-0.112$ ,  $p=0.339$ ). Stops resulted in a larger total gain of distance towards a goose's destination in spring (mean 20.7 km per track  $\pm$  22.6 SD, range= $-7.5$  to 80.5) than in autumn (mean 8.2 km  $\pm$  12.7 SD, range= $-17.9$  to 52.2; Wilcoxon rank sum test:  $W=204$ ,  $p=0.049$ ; Fig. 3). However, visually there was geographical variation in the trajectory shape of geese during (long) stops: whereas straight trajectories occurred in all regions at sea, circular trajectories mostly occurred around Bjørnøya, south of Edgeøya and off the Norway coast north of Tromsø (Supporting information).

## Discussion and conclusion

We studied the migration behaviour of 38 GPS-tracked pink-footed geese during the crossing of the Barents Sea and in relation to weather conditions in 2018–2020. We found that wind played an important role in many aspects of the crossings: the timing of the crossing initiation and of stops at sea, the deviation from the shortest route and thereby also the distance and duration of a crossing, ultimately affecting the duration and energetic costs of a crossing. Clear differences were found between spring and autumn: at crossing initiations, the availability of tailwinds was generally lower in autumn and geese displayed a higher selectivity for favourable winds. Also, en route, geese experienced higher wind support and migrated shorter and straighter in autumn than in spring, resulting in a shorter duration and lower total cost of the crossing.

The selectivity of pink-footed geese to initiate a sea crossing with wind support towards the destination indicates that geese start the crossing in circumstances that ease the crossing, especially in autumn. This is in line with the idea that birds should depart with winds in the direction of the intended destination (Åkesson and Hedenström 2000) and that favourable tailwinds initiate departures (Ma et al. 2011, Kölzsch et al. 2016, Becciu et al. 2019). In general, the benefits for birds of selecting favourable winds can be, among others, the reduction of mortality risk, time and/or energy expenditure. The mortality risk caused by adverse weather conditions probably plays a minor role, because geese

are waterbirds and able to stop at sea (Butler et al. 1998, Pennycuick et al. 1999, Griffin 2008, Hübner et al. 2010, Vissing et al. 2020). However, reducing the energy expenditure by selecting favourable winds could play a major role for geese, as preserving energy during migration is essential for capital breeders (Madsen et al. 2002, Nilsson et al. 2013, Klaassen et al. 2017). Reducing the time needed for a crossing can also be relevant, because departing late allows accumulation of more resources, but arriving early enables birds to occupy the best nesting sites and rear chicks when food quality is high (van der Graaf et al. 2006), although arriving too early is penalized by adverse conditions like snow cover (Forchhammer et al. 2002, Najafabadi 2017).

The fact that the apparent selectivity for favourable winds during crossing initiations was higher in autumn than in spring can result from several factors. First, in spring, availability of supportive winds on days other than the actual departure day may suggest that supportive winds are more common than in autumn. Second, in autumn, geese are not limited by the pressure of a well-timed arrival as they are in spring. Therefore, they have more opportunity to wait and select the best wind for departure although, in autumn, waterfowl may be 'pushed' into migration as they depart when the winter arrives, thus having limited possibilities to stay in the summer area any longer (Xu and Si 2019). Third, in autumn, geese may be more selective because their juvenile brood travels with them. For juveniles, the penalty of travelling in adverse wind (i.e. increased mortality and exhaustion) may be higher than for adults. Also, when comparing individual tracked geese in autumn, those with juvenile brood initiated crossings with slightly better wind support than geese without juvenile brood. This was, however, not significant, possibly because geese already select the best wind support, or because also geese without juveniles maximize their own chance of successful crossings. Moreover, migratory decisions in relation to individual family status may be masked because it may be more important for families to join a flock, even when it contains unsuccessful breeders.

However, during later stages of crossings, geese experienced lower wind support in both seasons. This again has several possible explanations. First, winds change en route. Geese that start with supportive winds have no guarantee of experiencing supportive winds for the whole crossing. Second, geese may drift more with the wind in earlier stages of a crossing (i.e. compensating less to head towards the destination) than later on. Early during a crossing, there is still a chance that winds change towards the destination, and thus there is no pressure to compensate for drift as long as the deviation from the shortest route remains limited. In later stages of the crossing, compensation becomes increasingly necessary to reach the destination (Alerstam 1979, Liechti 2006).

Further, in spring, geese experienced higher wind supports when deviating more from the shortest route. This again suggests that wind conditions in spring are less favourable than in autumn for crossing the Barents Sea. This also explains why geese deviated more from the shortest route and made 18% longer detours in spring than in autumn: namely, to

fly with more supportive winds. Apparently, geese do not compensate completely immediately when blown off track by wind, in line with the model of 'adaptive drift' allowing a compensation for wind drift towards the end of a crossing (Alerstam 1979, Vansteelant et al. 2017), as they still experienced larger crosswinds in spring than in autumn. Head- and crosswinds, in combination with flights above moving surfaces like water, can cause wind drift of migrating birds (Alerstam and Pettersson 1976, Alerstam and Hedenström 1998). As a result of these deviations, geese covered larger distances, took longer and spent more energy to cross the sea in spring than in autumn. This appears paradoxical as geese are expected to migrate faster and save energy in spring. However, time-pressure in spring also limits the opportunities for geese to wait for tailwinds. Moreover, the sea crossing is only part of the migration of pink-footed geese and for a good comparison of migration speeds the whole route should be considered, including fuelling times (Lindström et al. 2019). Seasonal differences in migration speed vary between species, with swan geese *Anser cygnoides*, for example, migrating faster in spring than autumn (Batbayar et al. 2013), bar-headed geese *A. indicus* showing no difference (Köppen et al. 2010) and greater white-fronted geese and Bewick's swans migrating slower in spring than autumn. For the latter two species, this is because they have to build up reserves for breeding in spring, but not in autumn (Nolet 2006, Kölzsch et al. 2016); and the swans are, in addition, limited by the retreating ice front (Nuijten et al. 2014).

In spring, not only were the ground distances of crossings larger and durations longer, but the ratio of air distance to ground distance (110%) was also higher than in autumn (76%). As a result, the total air distance was 1.9 times higher in spring than in autumn, because of the longer crossing distances and detours in spring. This means that the energetic costs for the sea crossing differ substantially between the seasons. This difference may be even larger, because geese in spring carry capital resources for breeding, which may increase the flight costs in spring further. To what extent flocking benefits and thermoregulatory costs in both seasons may alter this balance is not known.

Geese frequently stopped on water during a sea crossing in spring and autumn. Most importantly, winds during stops were more adverse (i.e. not blowing towards destination) than winds during flights. This suggests that geese select conditions for flying that ease the crossing, also en route. This is described as the 'sit and wait for favourable winds' strategy by Gauthreaux et al. (2005). This may save energy, while time saving is not likely given the relatively long duration of stops at sea (on average 50% of the total crossing duration) and the short duration in absolute sense (0.9 day). An additional small benefit of stops at sea appeared to be the continued movement of geese on the water, often in the direction of the migration destination. Even though speed was low ( $0.6 \text{ m s}^{-1}$ ), geese usually still gained 10–20 km as they spent on average 50% of the crossing time on the water. It is unknown whether the geese swim actively or whether this is only passive movement caused by sea currents. The presence of

circular and linear paths during stops, with circular paths concentrated in specific areas of the sea, suggest that passive movement by currents occurs. Further aspects of stops, such as thermoregulatory effects of cooling feet in the water, are unknown.

When correcting for these wind effects, geese were found to have a higher flight probability in spring than in autumn, again suggesting that geese are more time- and/or energy-limited in spring than autumn. Second, in spring, geese were more likely to continue flying during later stages of crossings, which was not the case in autumn. In autumn, geese had generally lower but constant flight probabilities throughout crossings. This indicates that, in spring, the balance between (expected) costs and benefits of waiting changes while geese approach Svalbard. In other words, during earlier stages of crossings in spring, waiting for better winds pays off as benign winds could carry geese far towards their destination. However, closer to Svalbard, the energy that can be saved by waiting for good winds decreases as the distance to destination is shorter. This suggests a priority shift during spring crossings of the Barents Sea, from energy minimization to time minimization.

Furthermore, we found that geese, during both seasons and independently of their parental status, mostly flew short distances (between stops at sea) of approximately 100 km, even though they are able to cover between 500 and 800 km non-stop by own power. Stopping at sea allows geese to manage energy expenditure and decrease the risk of exhaustion by prolonged flights, which land birds are not able to do. Also, in greater white-fronted geese increased energetic costs (by headwinds) led to the decision to rest (Kölzsch et al. 2016). We found that geese without a juvenile brood stopped a larger proportion of the crossing time than geese that had a brood. This was contrary to our expectation that juveniles are inexperienced and thus may need to stop to rest more. This may indicate that reaching foraging grounds sooner may be more important for juveniles on migration than resting more underway. This is in line with the result that geese with a juvenile brood flew more of their ground distance by own power than geese without juvenile brood (80% versus 65%, respectively).

Apart from reducing energy expenditure and countering exhaustion, stops at sea can enable geese to avoid disorientation in adverse weather conditions. Weather conditions like fog that obstruct the visibility and sun ultimately decrease the navigation capacity (Chiaradia et al. 2007, Newton 2007, Kirsch et al. 2015, Becciu et al. 2019, Panuccio et al. 2019). We showed that geese interrupted flights under a high relative air humidity, which is an indicator for fog. This is in line with the consensus that clear skies facilitate avian migration (Erni et al. 2002). Additionally, geese could use other clues for navigation above the sea, like geomagnetic fields (Zein et al. 2021) or wave patterns (Alerstam and Pettersson 1976). Here, we found that waves play an important role for the decision of geese whether to fly or rest at sea. Both the mean wave period and wave height determined flights in geese, suggesting that not only weather conditions but also



conditions at sea level are essential. Long and high waves appear to preclude stopping at sea. Also, the air temperature is relevant for geese as flight probabilities were lower in higher temperatures for both seasons. An explanation may be, first, that migrating birds avoid flying under high temperatures as they would suffer hyperthermia and lose water (Carmi et al. 1992, Guillemette et al. 2016). Second, there may be less thermal lift at higher air temperatures, as more thermal lift occurs when the air temperature is lower than the sea temperature (Woodcock 1975).

External transmitters can increase drag and by this the migration performance of birds (Pennycuik et al. 2012). In our study, we cannot completely exclude possible effects of the transmitters on the migratory behaviour of geese. But in our study all individuals were equipped with (the same model of) transmitters, and so seasonal comparisons can be made. Furthermore, as negative effects of transmitters on waterfowl such as geese tend to be small, and drag by neck collar transmitters might be less than by backpack transmitters (Lameris and Kleyheeg 2017), our results are expected to represent natural behaviour.

Adverse winds, which geese experienced mainly during spring, can cause geese to drift, after which they might become disoriented, as seemed to have happened to one tracked goose. This might increase the dispersal rate of geese to novel areas, where breeding might follow after spring migration, if the area is suitable. These wind effects causing 'exploration' might help geese to cope with rapidly changing conditions in the Arctic. Also, the wind conditions may change due to climate change (Carvalho et al. 2017, Zeng et al. 2019), rendering tracking studies highly relevant to understand potential threats and opportunities for birds migrating over a sea barrier to the Arctic.

In conclusion, the Barents Sea is a barrier for migrating pink-footed geese, which are capital breeders of the Arctic, flexible in coping with weather conditions and for which the importance of time and energy can shift en route. Seasonal differences in wind support, flying and stopping behaviour, and the pressure for a well-timed arrival make crossings in spring almost twice as energy costly for geese as in autumn.

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## Author contributions

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## Data availability statement

Data are available from the DataverseNL Digital Repository: <<https://doi.org/10.34894/BPECFA>> (Geisler et al. 2022).

## Supporting information

The Supporting information associated with this article is available with the online version.

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